1936, but was found with pollen cones during the past winter. Mr. A. D. Robertson furnished the writer with male reproductive specimens from this plant in January and February, 1941.

A male tree growing in the Botanical Garden of the University of California, Berkeley, was observed to be in reproductive condition in January, 1941, by Mr. Donald G. Nelson of that institution. The origin of this plant is not known to the writer. Aside from the dozen plants enumerated here, there are probably a number of other specimens in cultivation on private estates that represent original seedlings, which were distributed in the days before it was discovered that these plants are easily propagated.

University of Illinois, Urbana,
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THE TAXONOMIC STATUS OF MICROSTERIS GREENE

Herbert L. Mason

Perhaps no member of the Polemoniaceae has been so greatly misunderstood as the very polymorphic aggregate species, *Phlox gracilis* (Dougl.) Greene. It has been variously treated as a member of the following genera: *Gilia, Collomia, Phlox, Navarretia, Polemonium,* and is the type species of the genus, *Microsteris* Greene; it has been divided and subdivided into species, subspecies, varieties, subvarieties and forms within these genera according to the particular whim of the author treating it. The plant ranges from the Pacific Coast to the Rocky Mountains and from temperate Alaska south to Mexico, and recurs in the Southern Hemisphere in Bolivia, Chile, and Argentina. Essentially an early spring annual, it occurs from the coastal bluffs to timberline. The intent of the present paper is to deal only with the generic position of the aggregate species and not to be concerned with the status and disposition of the smaller taxonomic units. Therefore, the entire group of variants will be treated, for the present at least, as one large, polymorphic species.

The species was first collected by Douglas on the banks of the Spokane River [Washington] and given the manuscript name, *Collomia gracilis;* it was first described by Hooker (6) in 1829 under the name *Gilia gracilis* with *Collomia gracilis* Douglas cited as a synonym. In 1887 Greene (4) referred the species to the genus *Phlox* with the statement: "This interesting plant came to the knowledge of botanists some years in advance of *Phlox Drummondii* Hook. and its allies. It was at first a thing of dubious aspect, not at home either in *Gilia* or *Collomia.* But since the discovery of the Texan group of annual species of *Phlox* with peculiar habit, it must have been the mere force of custom which has kept men from seeing that it is an absolutely perfect congener of *Phlox Drummondii.*" In 1891 (7, p. 433) O. Kuntze, recognizing the page priority of *Navarretia* over *Gilia,* made a purely nomencla-

torial shift in the combination *Navarretia gracilis* (Dougl.) Kuntze. In 1898 Greene (5) erected the genus *Microsteris* recognizing as species seven segregates of *Phlox gracilis*. In so doing Greene stated: "At present I am disposed to adopt it as a principle that species with mucilaginous seeds are nowhere, in this family, to be placed as congeneric with such as have seeds devoid of the gummiferous coating. This implies the removal of my *Phlox gracilis* from the genus *Phlox*." In his description of *Microsteris* he states "Calyx, corolla, stamens and capsule wholly as in *Phlox*." Thus Greene's *Microsteris* hangs by the single character "mucilaginous seeds." In the same year O. Kuntze (8, p. 203) referred *Collomia gracilis* Dougl. to *Polemonium* by the simple statement: "P. Morenonsis OK (Collomia gracilis Dgl. non Polemonium gracile)." His reasons are forever hidden in parenthetical synonymy. We can dismiss without further comment the references to *Navarretia* and *Polemonium*. The reference by Douglas to *Collomia* is understandable. It was based upon superficial resemblance; furthermore, at that time the genus *Collomia* had not been clearly circumscribed in the light of the family as a whole. Our problem resolves itself into determining whether *Phlox gracilis* shall be retained in *Gilia* as interpreted by Hooker, be retained in *Phlox* as interpreted by Greene in 1887 or be placed in *Microsteris* following Greene's later interpretation. Of subsequent authors most have preferred to follow Asa Gray's adaptation of Hooker's treatment in a broad concept of the genus *Gilia* while only a few have used either *Phlox* or *Microsteris* when referring to this species. Brand (2) in his monograph of the Polemoniaceae with its highly elaborated system of "pigeon holes" chose to place *Phlox gracilis* in the genus *Gilia*, subgenus Benthamiophila, section Phlogastrum and proceeded to divide the species into fourteen entities in various subspecific categories. With respect to the generic position of the species I quote from Brand, "Species sic intermedia inter genera *Phlox* et *Gilia*, ut vix discernere possis, cui generi eam attribuas; a *Collomia* tamen, quacum plurimi autores junxerunt, calyce, ut cl. Greene docuit, valde diversa." Although he cited *Microsteris* as a synonym it is clear from the above quotation that he did not regard *Microsteris* as offering any problem. He was concerned with differentiating *Gilia* from *Phlox*. Here again we find but a single character utilized to place the species in *Gilia*, namely, the fact that the seeds develop mucilage when wetted. Other characters which it possesses that align it with *Phlox* are treated by Brand as exceptions in *Gilia*.

The most recent treatment that bears on this problem is that of Wherry (9) from whom we quote, "*Microsteris*. A few diminutive western annuals constitute this genus, which has been by various authors referred to *Collomia*, *Gilia* and *Phlox*. It shows little relationship with the first two genera, and in view of the difference in seeds can scarcely be congeneric with the last, although it may well be a derivative." Wherry, it will be seen, dismisses

Gilia and *Collomia* from consideration but parries between *Phlox* and *Microsteris*. He finally eliminates *Phlox* on the basis of "COROLLA-LIMB small; seeds becoming sticky when moistened," but he does at least suggest the responsibility of *Phlox* for the offspring. In an effort to validate the genus *Microsteris* another very insignificant character is added to the one previously utilized, namely the small size of the corolla limb.

It is perhaps a reasonable mode of escape when a group of plants does not fit comfortably in any of the related genera to erect a genus for it. However, this procedure should not be adopted until all of the evidence is carefully weighed to determine the precise nature of the differences that seem to make it necessary. As pointed out above *Microsteris* was erected by Greene who listed for it a single character difference from *Phlox*. Wherry's additional character of a small corolla limb adds scarcely anything of generic significance. The following tabular arrangement presents the facts pertaining to the development or non-development of mucilage or spiracles in the seed coats of most of the more widely accepted genera or Polemoniaceae.

Bonplandia: all species develop mucilage.

Cantua: a few species develop spiracles, the rest do not.

Cobaea: some species produce spiracles, and other species mucilage.

Gilia: very diverse, some species produce mucilage, others do not. The section *Ipomopsis,* recognized as a distinct genus by Wherry, is about equally divided in this respect.

Hugelia: some species produce mucilage, others do not.

Langloisia: all species produce mucilage.

Leptodactylon: in species examined none produce mucilage.

Linanthus: most species produce mucilage, some do not.

Loeselia: some produce mucilage, others do not.

Navarretia: some produce mucilage, others do not.

Phlox: as interpreted by Greene and by Wherry, does not produce mucilage, but if *Microsteris* is included, will be on the same basis as the other large genera.

Polemonium: some species produce mucilage, others do not.

The remaining few genera are each very small, and I have not as yet investigated them. But from the above data it would appear that the development of mucilage by the seed coat cannot be relied upon as of primary generic significance. All we can say of *Phlox* is that in the majority of species the seeds are immutable when wetted. This leaves as a character for the segregation of *Microsteris* only the small corolla limb. The magnitude of difference here, however, is no greater than the variational limits of corolla size in several other genera of Polemoniaceae, such as *Collomia, Navarretia* and *Linanthus.* This evidence, it seems, is just cause for denying generic status to *Microsteris.*

When we consider the characters that serve to keep the *Phlox gracilis* aggregate out of *Gilia* we turn from the flower and seed to

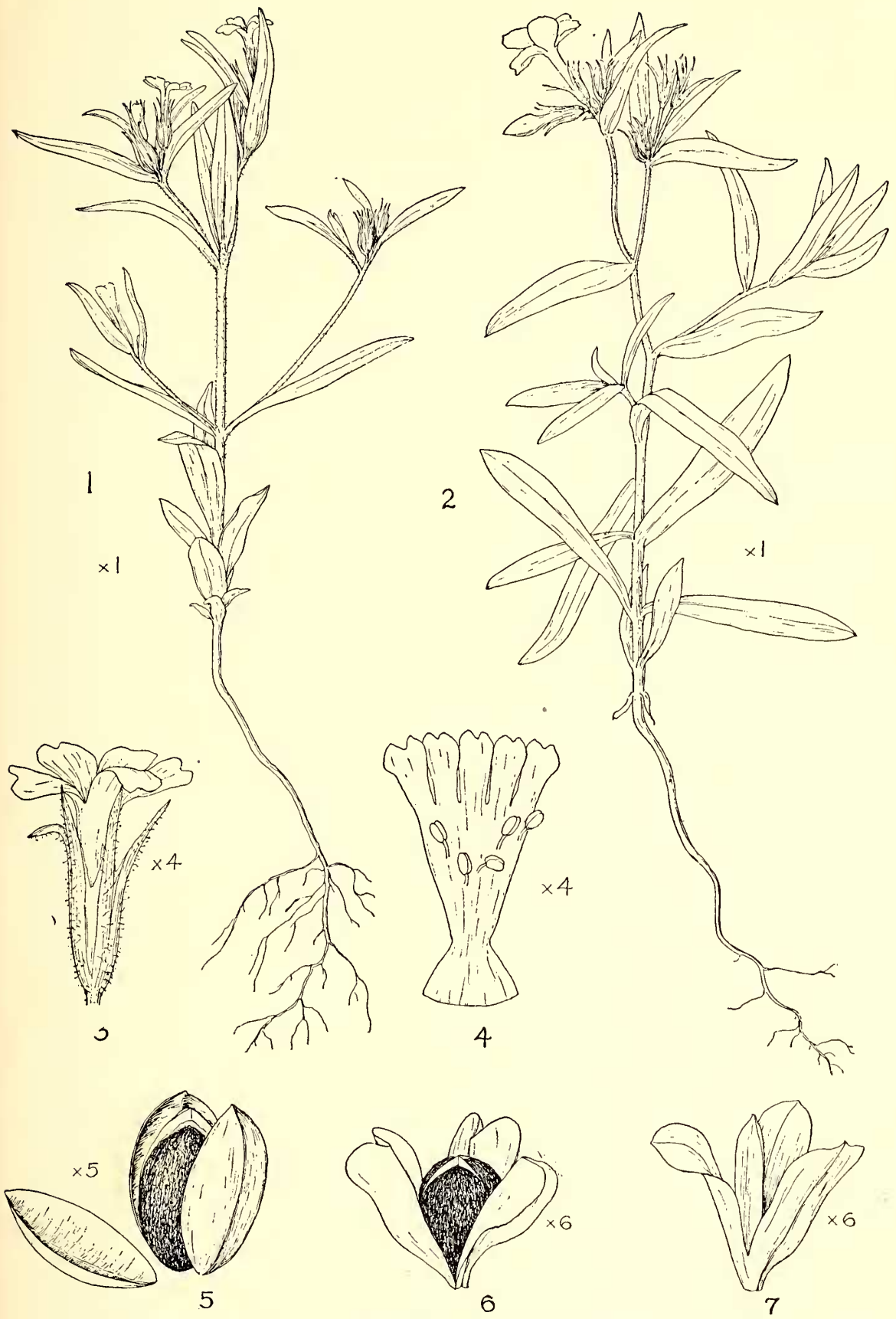

PLATE 12. COMPARISON OF PHLOX GRACILIS AND PHLOX DRUMMONDII VAR. TENUIS. FIG. 1. *Phlox gracilis.* FIG. 2. *Phlox Drummondii* var. *tenuis.* FIG. 3. *Phlox gracilis,* flower. FIG. 4. *Phlox gracilis,* opened corolla. FIG. 5. *Phlox gracilis,* capsule showing disarticulation of valves. FIG. 6. *Collomia,* capsule showing valves with margins reflexed. FIG. 7. Campanulate type of capsule found in many species of *Linanthus* and *Gilia.*

other parts of the plant. Of the authors who have referred the group to *Gilia* we find some who regard most of the small genera (*Linanthus, Hugelia, Gymnosteris, Loeselia, Collomia, Leptodactylon*) as belonging to this genus; others who recognize the small genera mentioned above but who have followed precedent in the disposition of *Phlox gracilis*. When we exclude from *Gilia* these small genera there still remains a polymorphic but closely related group of species. The leaves of this remaining group are normally alternate (occasionally through shortening of the internodes they may appear subopposite), and frequently pinnately toothed, lobed or dissected; the corolla lobes are normally entire; the stamens are usually, but not always, equally inserted and equal in length; the capsule valves do not disarticulate on dehiscence but remain united at the base, and although the valves may spread campanulately or sometimes reflex on the midvein the capsule falls as a whole (pl. 12, fig. 7); the locules of the ovary are usually more than one-seeded, but occasionally are one-seeded; the seeds are usually small and angular.

Phlox gracilis does not conform with *Gilia* as the following summary of its characters demonstrates: the leaves are predominately opposite (pl. 12, fig. 1), at least below, and are always linear, or oblong and entire; the corolla is salverform, the limb rotate, the lobes frequently emarginate (pl. 12, fig. 3); the stamens are unequally inserted and unequal in length (pl. 12, fig. 4); the capsule valves are rigid and disarticulate completely on dehiscence; the locules are one-seeded, the seeds large (pl. 12, fig. 5). Greene was quite correct when he said in his diagnosis of *Microsteris,* "Calyx, corolla, stamens and capsule wholly as in *Phlox.*" And of course Wherry accepts for this group a close relationship to *Phlox*. It seems that the presence of such typical *Phlox* characters as the rigid, disarticulating capsule valves and the solitary large seeds in the locules, together with several minor characters which are usual in *Phlox* and occasional or abnormal in *Gilia,* throw the weight of the argument to *Phlox,* not to *Gilia*.

Another line of evidence supporting a relationship with *Phlox* rather than with *Gilia* is found in cytological studies; the basic chromosome number in *Gilia* appears to be $n = 9$ while the basic chromosome number in *Phlox* is $n = 7$. In *Phlox gracilis* $2n = 14$, the count being made from root tip cells. However, in a group with such wide climatic tolerance and such great morphological diversity we may anticipate some polyploidy.

Botanists familiar with the genus *Phlox* only in western North America may be pardoned for hesitating to place *P. gracilis,* a plant so different from *P. Douglasii* and *P. adsurgens,* in the same genus. It is, as Greene points out, only when we take into consideration the range of variation of the entire genus that we can hope for a true picture of relationship. In this case the *Phlox Drummondii* complex of Texas offers a key to the relationship. A collection of *Phlox Drummondii* var. *tenuis* Gray from Texas

(*Lindheimer 468*) is an excellent example of a connecting type between *Phlox gracilis* and other members of the genus. A comparison of figures 1 and 2 (pl. 12) will at once show the great similarity in aspect between the two. Figure 1 represents a plant of *Phlox gracilis* collected at Tuolumne Meadows, Yosemite National Park, California (*Mason 4869*). It was especially selected for this comparison but is representative of a large segment of the *"Microsteris"* variants. The evidence of a general similarity of aspect substantiated by indisputable *Phlox* characters upholds Greene's first opinion of the generic position of this group.

The fact that this western group of plants is related to an eastern group by way of a southern bond is not inconsistent with the growing body of information now being accumulated relative to the history of vegetation in the southwest. Among other genera with related species showing a similar distribution pattern are *Juglans, Cercis, Forestiera* and *Fraxinus*. This group of trees and shrubs are all represented in fossil floras of Middle Tertiary time and today occur in savanna like floras where *Phlox gracilis* is a common associate. It would seem that these relationships go back at least as far as the Miocene, if not the Oligocene, in the Sierra Madrean flora of Axelrod (1). Perhaps this region has been the center of origin and differentiation of the entire Polemoniaceae. Certainly not all *Phlox* species have had their origin in Keewatin Land as postulated by Wherry (10). If this were true it would be reasonable to expect a higher development of the genus in the old world than is now evident, since migration routes through Beringia would have been available. The occurrence of *Phlox* in this northern region during the Pleistocene, north and west of the Keewatin center of glaciation is attested by fossil fruits reported and figured by Chaney and Mason (3 p. 17, figs. 34, 36). These specimens are strikingly similar to *P. sibirica* L., a species occurring in the Alaska region today, and ranging westward into Siberia.

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Literature Cited

1. Axelrod, D. A Miocene flora from the western border of the Mohave Desert. Carneg. Inst. Wash. Publ. 516. 1939.
2. Brand, A. [Polemoniaceae] in Engler, Pflanzenreich 4^{250}: 1–203. 1907.
3. Chaney, R. W., and H. L. Mason. A Pleistocene Flora from Fairbanks, Alaska. Amer. Mus. Nov. no. 887: 1–17. 1936.
4. Greene, E. L. New or noteworthy species. Pittonia 1: 139–143. 1887.
5. ———. Some western Polemoniaceae. Pittonia 3: 299–305. 1888.
6. Hooker, W. T. Bot. Mag. 56: t. 2924. 1829.
7. Kuntze, O. Rev. Gen. Pl. 1. 432–434. 1891.
8. ———. Rev. Gen. Pl. 3^{21}: 202–203. 1898.
9. Wherry, Edgar T. A provisional key to the Polemoniaceae. Bartonia 20: 14–17. 1940.
10. ———. Geographic relations in the genus Phlox. *Op. cit.* 20: 11–14. 1940.